Elsevier Editorial System(tm) for Brain and Cognition
Manuscript Draft

Manuscript Number: BRCG-14-94R1

Title: Social environment elicits lateralized navigational paths in two populations of typically developing children

Article Type: Regular Article

Keywords: Laterality, Cerebral Lateralization, Social Environment, Children

Corresponding Author: Dr. Gillian S Forrester,

Corresponding Author's Institution: University of Westminster

First Author: Gillian S Forrester

Order of Authors: Gillian S Forrester; Molly Crawley; Casey Palmer

Abstract: The current study provides the first evidence of human lateralized navigation of a social space within a naturalistic environment. We employed a quantitative, observational approach and report on a detailed set of nearly 700 independent navigational routes from two separate child populations consisting of over 300 typically developing children, aged five to fourteen years. The navigational path was considered across the sagittal plane (left, right) around three distinct target types (peer, adult and object). Both child populations expressed a significant bias for choosing a rightward navigational path around a human target (e.g. peer, adult) and no lateral preference for navigation around fixed, inanimate objects. A rightward navigational path provides an advantage for the left visual field and the right hemisphere, facilitating both the production and perception of social-emotion stimuli. The findings are consistent with evidence from studies of non-human animal species demonstrating that the social environment elicits predictable lateralized behavior, and support an early evolutionary delineation of functional processing by the two hemispheres.

UNIVERSITY OF WESTMINSTER

18th July 2014

Re: Manuscript BRCG-14-94

Dear Stephen Christman, Ph.D. (Action Editor),

Thank you for your feedback regarding our manuscript entitled: Social environment elicits lateralized navigational paths in two populations of typically developing children (BRCG-14-94). My co-authors and I are very pleased with the positive feedback with which we have been provided. We also appreciate the time and effort offered to evaluate our manuscript and recognize that this is a very busy time for many reviewers.

Please find the attached author responses to the specific suggestions for improvements. In addition to addressing the Reviewer and Editor comments, we have made some minor additional adjustments to the text to improve clarity and fluidity.

We hope that with these minor revisions, you now find our manuscript suitable for publication in Brain and Cognition.

We look forward to hearing back from you in due course.

Kind regards,
Gillian Forrester

Dr Gillian S Forrester
Senior Lecturer
Department of Psychology
University of Westminster

Contact Information **Gillian S. Forrester**
Senior Lecturer
Department of Psychology
University of Westminster
309 Regent Street
London, W1B 2UW
T +44(0) 20 7911 5000 ext. 69006
g.forrester@westminster.ac.uk

Reviewer comments and Author responses:

Comment: Reviewer 1 has suggested the insertion of the following reference on line 55: for fish see also De Santi et al. (2001). Mosquitofish display differential left- and right-eye use during mirror-image scrutiny and predator-inspection responses. Animal Behaviour, 61: 305-310.
Response: The text has been amended to include the citation provided above.

Comment: Reviewer 1 has suggested the correction of a citation on line 56: Robins et al. (1998)
Response: The text has been corrected to reflect the accurate date for this citation.

Comment: Reviewer 1 has suggested the insertion of the following reference on line 65: see also Rogers et al. 2013 (quoted in references at line 583)
Response: The text has been amended to include the citation provided above.

Comment: Reviewer 1 has suggested the insertion of the following reference on line 96: see also Vallortigara et al (2011). Brain asymmetry (animal). Wiley Interdisciplinary Reviews: Cognitive Science, 2: 146-157 DOI: 10.1002/wcs.100
Response: The text has been amended to include the citation provided above.

Comment: Reviewer 1 has suggested the insertion of the following reference on line 384: see also Siniscalchi et al. (2013). Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. Current Biology, 23: 2279-2282.
Response: The text has been amended to include the citation provided above.

Comment: Reviewer 1 has suggested the correction of the reference on line 565: please add reference to the journal: Current Biology, 17: 199-201.
Response: The text has been corrected to reflect the accurate journal, volume and page numbers for this citation.

Additional Amendments:
Line 63: insertion of omitted word ‘for’
Line 70: insertion of “:” after the word efficiency
Lines 116, 266, 371: amendment of ‘in press’ to ‘2014’ for reference: Quaresmini et al.
Line 118: insertion of phrase for clarity ‘…during spontaneous natural behaviors.’
Line 158-9: addition of reference: Fox et al., 2006
Line 161: addition of reference: Scott et al., 2009
Line 164: addition of reference: MacHale et al., 1989
Line 169: insertion of omitted word ‘position’
Lines 189-192: rewording of final sentence for fluidity
Line 287: rewording of final sentence for clarity
Line 413-415: insertion of sentence regarding evolution of cooperation for concluding remarks

Highlights

We report on a detailed set of lateralized navigational paths of children

Children demonstrated a right path bias for navigating around other humans

Children demonstrated no path bias for navigating around an object

A right path bias predicts a left visual field/right hemisphere dominance

The social environment elicits lateralized navigational behavior in typical children

Social environment elicits lateralized navigational paths in two populations of typically developing children

Gillian S. Forrester[a*], Molly Crawley[a], Casey Palmer[a]

[a]Department of Psychology, Faculty of Science and Technology, University of Westminster, 309 Regent Street, London, England, W1B 2UH

Author's contact details:

*Gillian S. Forrester: email: g.forrester@westminster.ac.uk; tel: +44 208 911 5000 x69006

Molly Crawley: email: molly.mae.crawley@my.westminster.ac.uk

Casey Palmer: ckp1@hotmail.co.uk

*Correspondence concerning this article should be addressed to Gillian S. Forrester, Department of Psychology, Faculty of Science and Technology, 309 Regent Street, University of Westminster, London, W1B 2UH

Contact: g.forrester@westminster.ac.uk

Abstract

The current study provides the first evidence of human lateralized navigation of a social space within a naturalistic environment. We employed a quantitative, observational approach and report on a detailed set of nearly 700 independent navigational routes from two separate child populations consisting of over 300 typically developing children, aged five to fourteen years. The navigational path was considered across the sagittal plane (left, right) around three distinct target types (peer, adult and object). Both child populations expressed a significant bias for choosing a rightward navigational path around a human target (e.g. peer, adult) and no lateral preference for navigation around fixed, inanimate objects. A rightward navigational path provides an advantage for the left visual field and the right hemisphere, facilitating both the production and perception of social-emotion stimuli. The findings are consistent with evidence from studies of non-human animal species demonstrating that the social environment elicits predictable lateralized behavior, and support an early evolutionary delineation of functional processing by the two hemispheres.

Keywords

Laterality, Cerebral Lateralization, Social Environment, Children

1. Introduction

A growing body of evidence across a range of animal species demonstrates a bias to keep conspecifics situated on their left side. A left eye bias to monitor conspecifics is widespread across a range of vertebrates including: fish (De Santi, et al., 2001; Sovrano et al., 2001), toads (Robins et al., 1998), lizards (Deckel, 1995; Hews and Worthington, 2001), pigeons (Nagy et al., 2010), chicks (Vallortigara, 1992; Vallortigara and Andrew, 1991) and beluga whales (Karenina et al., 2010), and may represent a common evolutionary behavioral manifestation reflective of a right hemisphere dominance for processing social stimuli and arousing situations (for a review, see Rosa Salva et al., 2012). The findings from these studies support a hypothesis that lateralized perceptual behaviors may have derived from an early delineation of a right hemisphere dominance for responding to unexpected and behaviorally relevant stimuli (e.g. predator) and a left hemisphere dominance for well learned sequences of actions (e.g. feeding) (MacNeilage et al., 2009; Rogers, 2000a; Rogers et al., 2013). This type of asymmetric behavioral activity might have an adaptive value, facilitating simple reflexive and automatic responses to increase the survival of individuals (Rutherford and Lindell, 2011). The appropriation of specialized processing to operate in parallel within the left and right hemispheres is thought to facilitate neural efficiency: allowing different functions to operate in parallel, decreasing the duplication of functioning across hemispheres and eliminating the initiation of simultaneous and incompatible responses (Rogers et al., 2004; Tommasi, 2009; Vallortigara and Rogers, 2005).

Right hemisphere dominance patterns have been reported for face perception and social recognition in a range of animal species. For example, a left gaze bias for face perception (e.g. looking time of centrally presented faces) has been reported in: sheep (Peirce et al., 2000), dogs and rhesus monkeys (Guo et al., 2009), chimpanzees (Morris and Hopkins, 1993), and humans (behavioral study: Burt and Perret, 1997; neuro-imaging: Kanwisher et al., 1998). A left motor bias (right hemisphere dominance) has also been reported for the production of facial expressions in marmosets (Hook-Costigan and Rogers, 1998) macaques (Hauser, 1993), baboons (Wallez and Vauclair, 2011) and in chimpanzees (Fernández-Carriba et al., 2002), indicating that both the perception and production of emotions may be preferentially controlled by the right hemisphere.

Nonhuman primates demonstrate an excellent animal model for understanding the evolutionary emergence of lateralized behaviors related to the social environment. There is little naturalistic evidence from field studies to align with those from other animal species discussed earlier. However, studies that consider spontaneous naturalistic, species-specific encounters in nonhuman primates have reported a left visual preference (right hemisphere dominance) during aggressive encounters in gelada baboons (Casperd and Dunbar, 1996) and in a zoo-housed group of mangabeys during spontaneous approach behaviors (Baraud et al., 2009), suggesting that rudimentary primitive avoidance behaviors controlled by the right hemisphere may have contributed to the emergence of negative emotions (Vallortigara and Rogers, 2005; Vallortigara et al., 2011).

Evidence from great ape studies has highlighted the importance of the social environment in modulating behavior during social interactions and situations involving increased arousal. High-ranking chimpanzees were approached significantly more frequently from their left visual hemifield suggesting the facilitation for the rapid identification of facial expressions and predictability of behaviors by the right hemisphere (Fernández-Carriba et al., 2002). Left biased motor asymmetries have also been associated with self-directed behaviours. For example, rehabilitated orangutans exhibited a significant group-level lateralized preference for left-handed scratching and for the fine manipulation of parts of the face (Rogers and Kaplan, 1995), and while self-directed scratching showed no hand preference in chimpanzees, there was a significant bias for scratching on the left side of the body (Hopkins, 2006). Forrester and colleagues (2011; 2012) noted an increase in left hand (right hemisphere) activity during the observation of naturalistic unimanual hand actions for self-directed behaviors and hand actions directed towards social partners compared with hand actions directed towards objects. In all cases, the authors postulated a right hemisphere dominant role in the processing of emotive and arousal-increasing stimuli.

A recent study by Quaresmini et al. (2014) aligns most closely with the evolution of social lateralization studies that indicate a preference to keep conspecifics proximally situated with a left visual field advantage during spontaneous natural behaviors. Observational focal sampling of spontaneous social behaviors in a family group of western lowland gorillas (Gorilla gorilla gorilla) and in a colony of captive zoo-living chimpanzees (Pan troglodytes), revealed group-level biases in both gorillas and chimpanzees (trend) for keeping conspecifics proximally situated to the left side of the focal individual compared with the right side. The authors suggest that lateral

positioning is likely to reflect a right hemisphere specialization for a heightened state of arousal associated with the detection of faces and facial expressions. These studies support the evolutionary perspective that the right hemisphere retains dominant control for behaviors associated with individual recognition, decoding other's intentions, and navigating the social hierarchical system (for a review, see Rosa Salva, et al., 2012). Moreover, findings from these studies suggest that the social environment may have been a critical pressure in aligning population behavior for predator defense and for cooperation (Ghirlanda et al., 2009; Ghirlanda and Vallortigara, 2004; Vallortigara and Rogers, 2005).

The study of human emotion processing has a long history in the literature, dominated by two prevailing theories of cerebral lateralization. The right hemisphere hypothesis (e.g. Borod et al., 1998; Campbell, 1982) proposes that the right hemisphere is solely responsible for the processing of emotion. Alternatively, the valence hypothesis (e.g. Davidson, 1995) purports that both the right and the left hemispheres are involved in affect processing, such that the left hemisphere is dominant for positive affect and the right hemisphere is dominant for negative affect. Although animal studies do not contradict the right hemisphere theory from an evolutionary perspective, evidence from non-human animal approach/avoidance behaviors tend to be more parsimonious with the valence theory. For example, birds (Franklin III and Lima, 2001; Koboroff et al., 2008; Rogers, 2000b), lizards (in the laboratory: Bonati et al., 2013; in the wild: Martín et al., 2010), and toads (Lippolis et al., 2002), have all been shown to manifest a left eye preference for well-learned sequences of actions (e.g. predator monitoring), but conversely, they demonstrate a rightward preference for responding to urgent situations (e.g. escaping from the dangerous stimulus). Additionally, in great apes, a

recent eye preference study found a left visual field /right hemisphere advantage for negative stimuli and right visual field/left hemisphere advantage for positive stimuli for viewing pictures (Braccini et al., 2012).

In humans, the valence theory model has gained some support from laboratory investigations. For example, the right hemisphere demonstrated greater activation than the left hemisphere in the region of the superior temporal sulcus associated with the processing of an approaching stranger with directed mutual gaze (Pelphrey et al., 2004). Additionally, right-handed people have been shown to respond more quickly to unexpected stimuli with their left hand compared with their right hand (e.g. Fox et al., 2006 reference). And, nonverbal, emotional vocalizations (e.g. cries and shouts) have demonstrated a right-hemisphere activation dominance in contrast to emotionally neutral vocalizations, which were biased to the left hemisphere (for a review see, Scott et al., 2009). Moreover, studies of brain damaged individuals suggest that people who incur left hemisphere trauma are more likely to become depressed than those who incur injury to the right hemisphere (e.g. MacHale et al., 1998). One theory is that the right hemisphere possesses a sensitive attentional system that responds selectively for novel and dangerous stimuli in the environment (for a review see Fox et al., 2006).

Social laterality has been little studied in the naturalistic behaviours of humans. The data that exists in this area suggest that mothers and fathers prefer to position their offspring on left side of their bodies (Nakamichi and Takeda, 1995; Scola and Vauclair, 2010a; Vauclair and Scola, 2009). While it is not proven that left arm cradling is associated with cerebral lateralization for the perception of emotion, the

physical positioning is thought to enable social-emotional feedback stimuli (e.g. gaze, facial expression) to maintain a direct route to the right hemisphere (for a review, see Scola and Vauclair, 2010b). This interpretation gains support from a study that indicated that children who were held with a left arm preference demonstrated a typical left visual field (right hemisphere) bias for faces on chimeric face tests, whereas individuals who were held with a right-arm lacked a visual field bias (Vervloed, et al., 2011). The ramification of hemispheric bilateralization for social-emotional processing has yet to be explored within the scope of cognitive development.

The influence of the social environment on lateralized behaviors has now been investigated across a wide variety of animal species. New evidence suggests that the social environment elicits lateralized motor behavior. Currently, there is a paucity of data relating to how humans navigate their environmental space, and investigations that consider the naturalistic context of the individual are rare. The current study provides the first report of lateralized social behaviors elicited by two populations of human children during naturalistic play. Extending upon human and animal studies of social laterality, this study observed the natural and spontaneous lateral navigational routes of children around adults, peers and objects in order to consider cerebral lateralization and lateralized motor action within the social environment.

2. Methods

2.1 Participants

All of the participants were observed unobtrusively in a naturalistic environment using an opportunity sampling method. Data relating to gender, age and handedness were not recorded. Only children were included in the study because it limits the influence of learnt social and cultural conventions. The procedures for this study involving human participants were in accordance with ethical standards of the responsible committee on human experimentation (institutional and national) and with the spirit of the Helsinki Declaration of 1975, as revised in 2000.

2.1.1 Participants C-Population

C-Population consisted of 101 individuals. Individuals were observed within a public play area, which contained equipment suitable for children up to a maximum of fourteen years of age.

2.1.2 Participants M-Population

M-Population consisted of approximately 200 children aged between four and eleven years. Individuals were observed within a school playground, (St Catherine's Primary School, Kent) which contained equipment suitable for children school children aged between 5-11 years.

2.2 Data capture

The study considered the observed naturalistic play behaviours of two separate populations of children (C-Population and M-Population) at different sites on

different dates and independently coded by two different raters (C and M). Data for C-Population were collected between March and April in 2013, while data for M-Population were collected between the January and February 2014.

Children were observed during naturalistic play for the assessment of navigational behaviours within the social environment. C-Population data were recorded over 3 visits for an average of 60 minutes visit, equalling a total of approximately 180 minutes and 340 events. M-Population data were recorded over 7 visits for an average of 25 minutes per visit equalling a total of 175 minutes and 348 events.

2.3 Data Coding

Two independent raters recorded observational data (C, M). Only information specifically related to lateral direction on a sagittal plane was recorded. A pen and paper recording method was adopted using a preformatted spread-sheet indicating variables to be recorded. The lateral path (left, right) that the observed child chose to navigate around stationary target (peer, adult, object) on order to reach a position accessible by a clear path on both sides and of approximately equal distance achieved by a left or right path was noted (Figure 1).

Figure 1.

- Insert Figure 1 -

Figure 1 illustrates the two possible navigational paths (left, right) of the observed child around a target (in this case a peer). A left or right navigational path inherently dictates the side of the body that will be presented to the individual around which the observed child navigates. In this case, a left navigational path presents the right side of the body and right visual field to the peer. A right navigational path presents the left side of the body and the left visual field to the peer.

Navigation around both peers and adults was considered. Additionally, a control condition was employed utilizing fixed, inanimate objects (e.g. large rubbish bin) in order to create the following 2x3 factor design: navigate left (adult), navigate left (peer), navigate left (object), navigate right (adult), navigate right (peer), navigate right (object). To control for confounding factors, each navigational path of an observed child began at a neutral point (approximately equidistant left or right from the desired location), and proceeded around (left or right) one of the target categories (adult, peer, object). The observed child and the target (peer, adult) were required to have directed gaze. If the observed child was navigating around a peer or adult that was facing away (gaze averted or obscured), the trial was excluded. Additionally, if a child began navigation from an ambiguous position (i.e. not equidistant from the desired goal location), the event was excluded from the analysis. Each navigational path was equal to one frequency point. In line with Quaresmini et al. (2014), to ensure that the relative presence of the social partner was influencing the positioning of the focal subject, we adopted an approximate distance of less than 3 m or less between the child being observed and the social partners.

Data collection method varied slightly between the two populations of children. For C-Population, a focal sampling approach was employed. Each focal follow lasted two minutes in duration. Data were included to the dataset if two minutes of continuous observation was completed. Stationery object targets consisted of a tree, a rubbish bin and an ornamental rock and remained consistent across all data collection visits. These objects were fixed at the entry point of the playground and required lateral navigation to access the playground equipment. These fixed items were chosen because they presented equal opportunity for navigation around both sides.

M-Population data collection consisted of an opportunity sampling of an entire school population. Each data point was collected based around a stationery target (adult, peer, object) used as a reference location. It was necessary that animate targets remained stationery throughout the observed child's navigational path to their desired location. Stationery object target was a rubbish bin. This object and its location remained consistent throughout all seven data collection visits. The bin was located at the intersection of two discrete segments of the playground, such that it was circumnavigated by the majority of the children during any given play session.

2.4 Data Analysis

A laterality index (LI), binomial tests, z-scores approximations of the binomial scores and a chi-square test were performed to assess population-level lateral biases. Additionally, peer and adult frequencies were collapsed within and between the two populations in order to consider the influence of animate and inanimate targets (e.g. Forrester et al. 2011; 2012; 2013). LI scores were calculated using the formula [LI =

(R-L)/(R+L)], with R and L being the frequency counts for right and left navigational path frequency counts. LI values vary on a continuum between -1.0 and +1.0, where the sign indicates the direction of hand preference. When R=L, then LI is zero. Positive values reflect a right navigational path preference while negative values reflect a left navigational path preference. The absolute value depicts the strength of hand preference. The directional strength of navigational path for each population was calculated using z-scores such that a population were left navigational path biased when $z \leq -1.96$, right navigational path biased when $z \geq 1.96$ and ambi-preferent for path direction when $-1.96 < z < 1.96$. All statistical tests were two-tailed (alpha < .05).

3. Results

Raw frequencies, binomial approximations of z-scores for each population and HI scores are presented in Table 1 by population (M Population, C Population and populations combined). Factors are displayed by target condition (peer, adult, object) and side (left, right).

Table 1 demonstrates raw frequencies, binomial approximations of z-scores and HI scores of unimanual lateralized hand actions.

- Insert Table 1 -

Because the binomial tests indicated that children navigated around both peers and adults with a significant bias of presenting their left side, in both populations, these two levels were collapsed for further statistical tests. A 2x2 chi-square test was

conducted on each population to consider target (human, object) and side (left, right). The M-Population revealed a significant interaction between target and side such that the children were biased towards a rightward navigational path around a peer, where as navigation around an object did not elicit a lateral bias $\chi^2(1, N = 101) = 5.27$, $p = .022$. Likewise, the C-Population revealed a significant interaction between target and side such that the children were biased towards a rightward navigational path around a peer, where as navigation around an object did not elicit a lateral bias $\chi^2(1, N = 200) = 11.7$, $p = .001$ (Figure 2).

Figure 2.

- Insert Figure 2 -

Figure 2 demonstrates the total frequencies by each population for target type (human, object) and navigation path (left, right).

Since both populations resulted in a significant bias for children choosing a right path to navigate human targets, a further chi-square test was conducted on the pooled data from both populations to demonstrate the robustness of the pattern, $\chi^2(1, N = 301) = 20.22$, $p < .000$ (Figure 3).

Figure 3.

- Insert Figure 3 -

Figure 3 illustrates the total frequencies by the combined population for target type (human, object) and navigation path (left, right).

4. Discussion

The present study considered the lateral navigational paths of children within a naturalistic setting to align with investigations of social lateralization in observational animal studies. Two populations of children were assessed by different observers at different locations, and at different times. Analyses revealed that both populations expressed a significant population-level bias for choosing a rightward navigational path around a human compared with a leftward navigational path. Additionally, neither population expressed a significant bias for a lateral preference when navigating around an object. These findings are to be considered in light of evolutionary theories for cerebral lateralization.

A bias for a right navigational path inherently implies that the navigating child is presenting the stationary target with the left side of the body. This social positing could impact upon both the production and perception of emotion processing. In the first instance, a bias to keep conspecifics on the left side inherently provides an advantage for viewing social stimuli with the left visual field. The left visual field would provide the most efficient route to the right hemisphere for processing identity, intention and angry or fearful facial expressions. This is consistent with animal studies that have demonstrated a left eye/right hemisphere preference bias for to monitoring familiar versus unfamiliar conspecifics (domestic chick: Deng and Rogers, 2002; Vallortigara and Andrew, 1991; Vallortigara et al., 2001; fish: Brown et al.,

2007; Sovrano, 2004; chimpanzees and gorillas: Quaresmini et al. 2014).
Additionally, a bias of the left visual field/right hemisphere has been reported in recognizing faces and facial expressions in both apes (Morris and Hopkins, 1993) and humans (De Renzi et al., 1994; Kanwisher et al., 1998). Within this context, exposing the left side of the body to conspecifics might be advantageous during novel or urgent situations to execute physical behaviors for protection and locomotion escape behaviors. In the second instance, the left side of the face in non-human primates has been reported to display emotive expression both earlier and more intensely than the right side of the face (Fernández-Carriba et al., 2002; Hauser, 1993; Hook-Costigan and Rogers, 1998). This lateral positioning may reflect a strategy to clearly display arousal status in order to inhibit extreme aggressive behavioral responses (Baraud et al., 2009).

Although approaching and withdrawing beahviours are well documented across animal species (Davidson et al., 1990; Quaranta et al., 2007; Siniscalchi et al., 2013), little is still known about how this behavior manifests in modern humans. Modern humans represent an animal species with an extremely complex social system. Many of our conscious motor actions related to approaching individuals are shaped and influenced by culture and social convention (e.g. hand shakes, kissing, etc.). However, our automatic motor actions may still represent evolutionary primitive patterns of behavior that are underpinned by cerebral specialization of the two hemispheres. Moreover, the display of these population-level lateralized behaviours (e.g. bias for keeping conspecifics in the left visual field) may be rooted in social species and facilitates the social communication and the prediction of social responses (Ghirlanda and Vallortigara, 2004; Vallortigara and Rogers, 2005).

Studies of cerebral lateralization indicate that the dominant functions are not solely processed by a single hemisphere. For example, studies of processing social stimuli also indicate small contributions from the left hemisphere: Meng et al., 2012), monkeys (Broad et al., 2000; Guo et al., 2009; Hamilton and Vermeire, 1988; Pinsk et al., 2005), dogs (Guo et al., 2009), and sheep (Peirce et al., 2000; Peirce and Kendrik, 2002). Therefore, there are limitations to the extent with which we can attribute a single function to a single hemisphere. Additionally, more detailed studies on lateralized motor biases are necessary at the individual level to shed further light on the association between cerebral lateralization of function and contralateral motor action. Nevertheless, evidence from a wide range of animal species of hemispheric dominance for specific functions has proven to be an informative behavioral marker of brain organization (e.g. MacNeilage et al. 2009).

Understanding how individuals navigate social networks may shed light on how and which environmental pressures helped to shape modern human social behavior. Specifically, the environment may have been a critical pressure in aligning population behavior for social actions requiring cooperation (Ghirlanda et al., 2009; Ghirlanda and Vallortigara, 2004; Vallortigara and Rogers, 2005). Additionally, future studies may consider the evaluation of the cognitive abilities of individuals with lateralized social navigation behaviors compared with individuals who do not express lateralized social navigation behaviors. It has been reported that stronger lateral motor dominance (e.g. handedness) correlates with the successful hemispheric specialization for language (Toga and Thompson, 2003). The present findings suggest that the environment elicits predictable behavior for social navigation that facilitates both the

production and perception of social-emotion stimuli in typically developing children. Therefore, the identification of individuals lacking lateralized social navigations behaviors may allow for the early targeting of individuals with cognitive delays and/or disorders.

Acknowledgements

We are grateful to the parents, teachers and children of St. Catherine's Primary School, Kent, for their participation in this investigation. Additionally, we gratefully acknowledge funding support provided in part the University of Westminster's Psychology Publication Stimulus Scheme.

References

1. Baraud, I., Buytet, B., Bec, P., Blois-Heulin, C., 2009. Social laterality and 'transversality' in two species of mangabeys: Influence of rank and implication for hemispheric specialization. Behavioural Brain Research, 198, 449–458. doi:10.1016/j.bbr.2008.11.032
2. Bonati, B., Csermely, D., Sovrano, V.A., 2013. Looking at a predator with the left or right eye: Asymmetry of response in lizards. Laterality: Asymmetries of Body. Brain and Cognition. 18, 329–339. doi:10.1080/1357650X.2012.673623
3. Borod, J.C., Cicero, B.A., Obler, L.K., Welkowitz, J., Erhan, H.M., Santschi, C., . . . Whalen, J.R., 1998. Right hemisphere emotional perception: Evidence across multiple channels. Neuropsychology. 12, 446–458. doi:10.1037/0894-4105.12.3.446

4. Braccini, S.N., Lambeth, S.P., Schapiro, S.J., Fitch, W.T., 2012. Eye preferences in captive chimpanzees. Animal Cognition. 15, 971–978. doi:10.1007/s10071-012-0523-9
5. Broad, K.D., Mimmack, M.L., Kendrick, K.M., 2000. Is right hemispheric specialization for face discrimination specific to humans? European Journal of Neuroscience
6. Brown, C., Western, J., Braithwaite, V.A., 2007. The influence of early experience on, and inheritance of, cerebral lateralization. Animal Behaviour. 74, 231-238. doi: 10.1016/j.anbehav.2006.08.014
7. Burt, D.M., Perret, D.I., 1997. Perceptual asymmetries in judgments of facial attractiveness, age, gender, speech and expression. Neuropsychologia. 35, 685–693. doi:10.1016/S0028-3932(96)00111-X
8. Campbell, R., 1982. Asymmetries in moving faces. British Journal of Psychology. 73, 95–103. doi:10.1111/j.2044-8295.1982.tb01794.x
9. Casperd, J.M., Dunbar, R.I.M., 1996. Asymmetries in the visual processing of emotional cues during agonistic interactions by gelada baboons. Behavioural Processes. 37, 57–65. doi:10.1016/0376-6357(95)00075-5
10. Daisley, J.N., Regolin, L., Vallortigara, G., 2010. Logic in an asymmetrical (social) brain: Transitive inference in the young domestic chick. Social Neuroscience. 5, 309–319. doi:10.1080/17470910903529795
11. Davidson, R.J. 1995. Cerebral asymmetry, emotion, and affective style, in: Davidson, R.J., Hugdahl, K. (Eds.), Brain asymmetry. MIT Press, Cambridge, MA, pp. 361–387.
12. Davidson, R.J., Ekman, P., Saron, C.D., Senulis, J.A., Friesen, W.V., 1990. Approach-withdrawal and cerebral asymmetry: Emotional expression and brain

physiology I. Journal of Personality and Social Psychology. 58, 330–341. doi:10.1037/0022-3514.58.2.330

13. De Renzi, E., Perani, D., Carlesimo, G.A., Silveri, M.C., Fazio, F., 1994. Prosopagnosia can be associated with damage confined to the right hemisphere: An MRI and PET study and a review of the literature. Neuropsychologia. 32, 893–902. doi:10.1016/0028-3932(94)90041-8
14. De Santi, A., Sovrano, A., Bisazza, G., Vallortigara, G. 2001. Mosquitofish display differential left- and right-eye use during mirror-image scrutiny and predator-inspection responses. Animal Behaviour. 61, 305-310.
15. Deckel, A.W., 1995. Lateralization of aggressive responses in Anolis. Journal of Experimental Zoology. 272, 194–200.
16. Deng, C., Rogers, L.J., 1997. Differential contributions of the two visual pathways to functional lateralization in chicks. Behavioural Brain Research. 87:173–82.
17. Fernández-Carriba, S., Loeches, A., Morcillo, A., Hopkins, W.D., 2002. Functional asymmetry of emotions in primates: New findings in chimpanzees. Brain Research Bulletin. 57, 561–564. doi:10.1016/S0361-9230(01)00685-2
18. Forrester, G.S., Leavens, D.A., Quaresmini, C., Vallortigara, G., 2011. Target animacy influences gorilla handedness. Animal Cognition. 14, 903–907. doi:10.1007/s10071-011-0413-6
19. Forrester, G.S., Quaresmini, C., Leavens, D.S., Spiezio, C., Vallortigara, G., 2012. Target animacy influences chimpanzee handedness. Animal Cognition. 15(6):1121-7.

20. Fox, M.D., Corbetta, M., Snyder, A.Z., Vincent, J.L., Raichle, M.E., 2006. Spontaneous neuronal activity distinguishes human dorsal and ventral attentional systems. PNAS. 103(35):10046–10051. doi**:**10.1073/pnas.0606682103
21. Frasnelli, E., Vallortigara, G., Rogers, L.J., 2012. Left-right asymmetries of behaviour and nervous system in invertebrates. Neuroscience & Biobehavioral Reviews. 36, 1273–1291. doi:10.1016/j.neubiorev.2012.02.006.
22. Franklin III, W.E., Lima, S.L., 2001. Laterality in avian vigilance: Do sparrows have a favourite eye? Animal Behaviour. 62, 879–885. doi:10.1006/anbe.2001.1826
23. Ghirlanda, S., Vallortigara, G., 2004. The evolution of brain lateralization: A game theoretical analysis of population structure. Proceedings of the Royal Society B: Biological Sciences. 271, 853–857. doi:10.1098/rspb.2003.2669
24. Ghirlanda, S., Frasnelli, E., Vallortigara, G., 2009. Intraspecific competition and coordination in the evolution of lateralization. Philosophical Transactions of the Royal Society B: Biological Sciences. 364, 861–866. doi:10.1098/rstb.2008.0227
25. Guo, K., Meints, K., Hall, C., Hall, S., Mills, D., 2009. Left gaze bias in humans, rhesus monkeys and domestic dogs. Animal Cognition. 12, 409–418. doi:10.1007/s10071-008-0199-3
26. Hamilton, C.R., Vermeire, B.A., 1988. Complementary hemispheric specialization in monkeys. Science. 242, 1691–1694. doi:10.1126/science.3201258
27. Hauser, M.D., 1993. Right hemisphere dominance for the production of facial expression in monkeys. Science. 261, 475–477. doi:10.1126/science.8332914
28. Hews, D.K., Worthington, R.A., 2001. Fighting from the right side of the brain: Left visual field preference during aggression in free-ranging male lizards

519 (Urosaurus ornatus). Brain, Behavior and Evolution. 58, 356–361.
520 doi:10.1159/000057576
521 29. Hook-Costigan, M.A., Rogers, L.J., 1998. Lateralized use of the mouth in
522 production of vocalizations by marmosets. Neuropsychologia. 36, 1265–1273.
523 doi:10.1016/S0028-3932(98)00037-2
524 30. Hopkins W.D., 2006. Lateralized Scratching in Chimpanzees (Pan troglodytes):
525 Evidence of a Functional Asymmetry During Arousal. Emotion. 6(4), 553-559.
526 31. Hopkins, W.D., 2004. Laterality in maternal cradling and infant positional biases:
527 Implications for the development and evolution of hand preferences in nonhuman
528 primates. International Journal of Primatology. 25, 1243–1265.
529 doi:10.1023/B:IJOP.0000043961.89133.3d
530 32. Kanwisher, N., Tong, F., Nakayama, K., 1998. The effect of face inversion on the
531 human fusiform face area. Cognition. 68, B1–B11. doi:10.1016/S0010-
532 0277(98)00035-3
533 33. Karenina, K., Giljov, A., Baranov, V., Osipova, L., Krasnova, V., Malashichev,
534 Y. 2010. Visual laterality of calf-mother interactions in wild whales. PLoS One,
535 5, e13787. doi:10.1371/journal.pone.0013787
536 34. Koboroff, A., Kaplan, G., Rogers, L.J. 2008. Hemispheric specialization in
537 Australian magpies (Gymnorhina tibicen) shown as eye preferences during
538 response to a predator. Brain Research Bulletin. 76, 304-306.
539 doi:10.1016/j.brainresbull.2008.02.015
540 35. Leavens, D.A., Aureli, F., Hopkins, W.D. 2004. Behavioral evidence for the
541 cutaneous expression of emotion in a chimpanzee (Pan troglodytes). Behaviour.
542 141, 979–997. doi:10.1163/1568539042360189

543 36. Lippolis, G., Bisazza, A., Rogers, L.J., Vallortigara, G., 2002. Lateralisation of
544 predator avoidance responses in three species of toads. Laterality: Asymmetries
545 of Body, Brain and Cognition. 7, 163–183. doi:10.1080/13576500143000221
546 37. Machale, S.M., O'Rourke, S.J., Wardlaw, J.M., Martin, S.D., 1998. Depression
547 and its relation to lesion location after stroke. Journal of Neurology,
548 Neurosurgery & Psychiatry. 64, 371-375. doi:10.1136/jnnp.64.3.371
549 38. MacNeilage, P.F., Rogers, L.J., Vallortigara, G., 2009. Origins of the left and
550 right brain. Scientific American. 301, 60–67.
551 doi:10.1038/scientificamerican0709-60
552 39. Martín, J., López, P., Bonati, B., Csermely, D., 2010. Lateralization when
553 monitoring predators in the wild: A left eye control in the common wall lizard
554 (Podarcis muralis). Ethology. 116, 1226–1233. doi:10.1111/j.1439-
555 0310.2010.01836.
556 40. Meng, M., Cherian, T., Singal, G., Sinha, P. 2012. Lateralization of face
557 processing in the human brain. Proceedings of the Royal Society B: Biological
558 Sciences. 279, 2052–2061. doi:10.1098/rspb.2011.1784
559 41. Morris, R.D., Hopkins, W.D., 1993. Perception of human chimeric faces by
560 chimpanzees: Evidence for a right hemisphere advantage. Brain and Cognition.
561 21, 111–122. doi:10.1006/brcg.1993.1008
562 42. Nagy, M., Àkos, Z., Biro, D., Vicsek, T., 2010. Hierarchical group dynamics in
563 pigeon flocks. Nature. 464, 890 – 893. doi:10.1038/nature08891
564 43. Nakamichi, M., Takeda, S., 1995. A child-holding thought experiment: Students
565 prefer to imagine holding an infant on the left side of the body. Perceptual and
566 Motor Skills. 80, 687–690.

44. Peirce, J.W., Kendrik, K.M., 2002. Functional asymmetry in sheep temporal cortex. Neuroreport. 13, 2395–2399. doi:10.1097/00001756-200212200-00004

45. Peirce, J.W., Leigh, A.E., Kendrick, K.M., 2000. Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. Neuropsychologia. 38, 475–483. doi:10.1016/S0028-3932(99)00088-3

46. Pelphrey, K. Al, Viola, R.J., McCarthy, G., 2002. When Strangers Pass: Processing of Mutual and Averted Social Gaze in the Superior Temporal Sulcus. Psychological Science. 15(9), 598-603.

47. Pinsk, M.A., DeSimone, K., Moore, T., Gross, C.G., Kastner, S. 2005. Representations of faces and body parts in macaque temporal cortex: A functional MRI study. PNAS Proceedings of the National Academy of Sciences of the United States of America.102, 6996–7001. doi:10.1073/pnas.0502605102

48. Quaranta, A., Siniscalchi, M., & Vallortigara, G. (2007). Asymmetric tail-wagging responses by dogs to different emotive stimuli. Current Biology. 17, 199-201.

49. Quaresmini, C., Forrester, G.S., Speizio, C., Vallortigara, G., 2014. Social environment elicits lateralized behaviours in gorillas and chimpanzees. Journal of Comparative Psychology. Online First. doi: 10.1037/a0036355

50. Robins, A., Lippolis, G., Bisazza, A., Vallortigara, G., Rogers, L.J., 1998. Lateralized agonistic responses and hindlimb use in toads. Animal Behaviour. 56, 875–881. doi:10.1006/anbe.1998.0877

51. Rogers, L.J., 2000a. Advantages and disadvantages of lateralization, in: Rogers, L.J., Andrew, R.J. (Eds.), Comparative vertebrate lateralization. Cambridge University Press. Cambridge, pp. 126–153.

591 52. Rogers, L.J., 2000b. Evolution of hemispheric specialization: Advantages and
592 disadvantages. Brain and Language. 73, 236–253. doi:10.1006/brln.2000.2305
593 53. Rogers, L.J., Kaplan, G., 1996. Hand preferences and other lateral biases in
594 rehabilitated orang-utans, Pongo pygmaeus pygmaeus Animal Behaviour. 51, 13–
595 25. doi:10.1006/anbe.1996.0002
596 54. Rogers L.J., Zucca P., Vallortigara G., 2004. Advantages of having a lateralized
597 brain. Proceedings of the Royal Society. B;271(6), S420–2.
598 55. Rogers, L.J., Vallortigara, G., Andrew, R.J., 2013. Divided brains. The biology
599 and behaviour of brain asymmetries. Cambridge University Press, New York,
600 NY. doi:10.1017/CBO9780511793899
601 56. Rosa Salva, O., Regolin, L., Mascalzoni, E., Vallortigara, G., 2012. Cerebral and
602 behavioural asymmetry in animal social recognition. Comparative Cognition &
603 Behavior Reviews. 7, 110–138. doi:10.3819/ccbr.2012.70006
604 57. Rutherford, H.J.V., Lindell, A.K., 2011. Author reply: More than evaluation:
605 Lateralization of the neural substrates supporting approach and avoidance
606 motivational systems. Emotion Review. 3, 347–348.
607 doi:10.1177/1754073911402404
608 58. Salk, L., 1960. The effects of normal heartbeat sound on the behavior of the
609 newborn infant: Implications for mental health. World Mental Health. 12, 168–
610 175.
611 59. Scola, C., 2009. L'importance de la relation me`re-enfant sur le coˆte. de portage
612 d'un jeune enfant [The importance of mother–infant relationship for holding-side
613 preferences]. Enfance. 61, 433–457.
614 60. Scola, C., Vauclair, J., 2010a. Infant's holding side biases by fathers in maternity
615 hospitals. Journal of Reproductive and Infant Psychology. 28, 3–10.

61. Scola, C., Vauclair, J., 2010b. Is infant holding-side bias related to motor asymmetries in mother and child? Developmental Psychobiology. 52, 475–486.
62. Scott, S.K., Sauter, D., McGettigan, C., 2009. Brain mechanisms for processing perceived emotional vocalizations in humans, in: Brudzynski S.M. (Ed), Handbook of mammalian vocalization: An integrative neuroscience approach. Academic Press, London, pp. 187-198.
63. Siniscalchi et al. (2013). Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. Current Biology, 23: 2279-2282.
64. Sovrano, V.A., (2004). Visual lateralization in response to familiar and unfamiliar stimuli in fish. Behavioural Brain Research. 152, 385–391. doi:10.1016/j.bbr.2003.10.022
65. Sovrano, V., Bisazza, A., Vallortigara, G., 2001. Lateralization of response to social stimuli in fishes: A comparison between different methods and species. Physiology & Behavior. 74, 237–244. doi:10.1016/S0031-9384(01)00552-2
66. Toga, A.W., Thompson, P.M., 2003. Mapping brain asymmetry. Nature Reviews Neuroscience. 4,37–48.
67. Tommasi, L., 2009. Mechanisms and functions of brain and behavioural asymmetries. Philosophical Transactions of the Royal Society B. 364, 855–9.
68. Vallortigara, G., 1992. Right hemisphere advantage for social recognition in chicks. Neuropsychologia. 30, 761–768. doi:10.1016/0028-3932(92)90080-6
69. Vallortigara, G., Andrew, R.J., 1991. Lateralization of response to change in a model partner by chicks. Animal Behaviour. 41, 187–194. doi:10.1016/S0003-3472(05)80470-1
70. Vallortigara, G., Cozzuti, C., Tommasi, L., Rogers, L.J., 2001. How birds use their eyes: Opposite left-right specialization for the lateral and frontal visual

641 hemifield in the domestic chick. Current Biology. 11, 29–33. doi:10.1016/S0960-
642 9822(00)00027-0
643 71. Vallortigara, G., Rogers, L.J., 2005. Survival with an asymmetrical brain:
644 Advantages and disadvantages of cerebral lateralization. Behavioral and Brain
645 Sciences. 28, 575–589. doi:10.1017/S0140525X05000105
646 72. Vallortigara, G., Chiandetti, C., Sovrano, V.A. 2011. Brain asymmetry (animal).
647 Wiley Interdisciplinary Reviews: Cognitive Science. 2, 146-157 DOI:
648 10.1002/wcs.100
649 73. Vervloed, M.P.J., Hendriks, A.W., van den Eijnde, E., 2011. The effects of
650 mothers' past infant-holding preferences on their adult children's face processing
651 lateralisation. Brain and Cognition. 75(3), 248-54. doi:
652 10.1016/j.bandc.2011.01.002
653 74. Wallez, C., Vauclair, J. 2011. Right hemisphere dominance for emotion
654 processing in baboons. Brain and Cognition. 75, 164–169. doi:
655 10.1016/j.bandc.2010.11

Social environment elicits lateralized navigational paths in two populations of typically developing children

Gillian S. Forrester[a*], Molly Crawley[a], Casey Palmer[a]

[a]Department of Psychology, Faculty of Science and Technology, University of Westminster, 309 Regent Street, London, England, W1B 2UH

Author's contact details:

*Gillian S. Forrester: email: g.forrester@westminster.ac.uk; tel: +44 208 911 5000 x69006

Molly Crawley: email: molly.mae.crawley@my.westminster.ac.uk

Casey Palmer: ckp1@hotmail.co.uk

*Correspondence concerning this article should be addressed to Gillian S. Forrester, Department of Psychology, Faculty of Science and Technology, 309 Regent Street, University of Westminster, London, W1B 2UH

Contact: g.forrester@westminster.ac.uk

Abstract

The current study provides the first evidence of human lateralized navigation of a social space within a naturalistic environment. We employed a quantitative, observational approach and report on a detailed set of nearly 700 independent navigational routes from two separate child populations consisting of over 300 typically developing children, aged five to fourteen years. The navigational path was considered across the sagittal plane (left, right) around three distinct target types (peer, adult and object). Both child populations expressed a significant bias for choosing a rightward navigational path around a human target (e.g. peer, adult) and no lateral preference for navigation around fixed, inanimate objects. A rightward navigational path provides an advantage for the left visual field and the right hemisphere, facilitating both the production and perception of social-emotion stimuli. The findings are consistent with evidence from studies of non-human animal species demonstrating that the social environment elicits predictable lateralized behavior, and support an early evolutionary delineation of functional processing by the two hemispheres.

Keywords

Laterality, Cerebral Lateralization, Social Environment, Children

1. Introduction

A growing body of evidence across a range of animal species demonstrates a bias to keep conspecifics situated on their left side. A left eye bias to monitor conspecifics is widespread across a range of vertebrates including: fish (De Santi, et al., 2001; Sovrano et al., 2001), toads (Robins et al., 1998), lizards (Deckel, 1995; Hews and Worthington, 2001), pigeons (Nagy et al., 2010), chicks (Vallortigara, 1992; Vallortigara and Andrew, 1991) and beluga whales (Karenina et al., 2010), and may represent a common evolutionary behavioral manifestation reflective of a right hemisphere dominance for processing social stimuli and arousing situations (for a review, see Rosa Salva et al., 2012). The findings from these studies support a hypothesis that lateralized perceptual behaviors may have derived from an early delineation of a right hemisphere dominance for responding to unexpected and behaviorally relevant stimuli (e.g. predator) and a left hemisphere dominance for well learned sequences of actions (e.g. feeding) (MacNeilage et al., 2009; Rogers, 2000a; Rogers et al., 2013). This type of asymmetric behavioral activity might have an adaptive value, facilitating simple reflexive and automatic responses to increase the survival of individuals (Rutherford and Lindell, 2011). The appropriation of specialized processing to operate in parallel within the left and right hemispheres is thought to facilitate neural efficiency: allowing different functions to operate in parallel, decreasing the duplication of functioning across hemispheres and eliminating the initiation of simultaneous and incompatible responses (Rogers et al., 2004; Tommasi, 2009; Vallortigara and Rogers, 2005).

Right hemisphere dominance patterns have been reported for face perception and social recognition in a range of animal species. For example, a left gaze bias for face perception (e.g. looking time of centrally presented faces) has been reported in: sheep (Peirce et al., 2000), dogs and rhesus monkeys (Guo et al., 2009), chimpanzees (Morris and Hopkins, 1993), and humans (behavioral study: Burt and Perret, 1997; neuro-imaging: Kanwisher et al., 1998). A left motor bias (right hemisphere dominance) has also been reported for the production of facial expressions in marmosets (Hook-Costigan and Rogers, 1998) macaques (Hauser, 1993), baboons (Wallez and Vauclair, 2011) and in chimpanzees (Fernández-Carriba et al., 2002), indicating that both the perception and production of emotions may be preferentially controlled by the right hemisphere.

Nonhuman primates demonstrate an excellent animal model for understanding the evolutionary emergence of lateralized behaviors related to the social environment. There is little naturalistic evidence from field studies to align with those from other animal species discussed earlier. However, studies that consider spontaneous naturalistic, species-specific encounters in nonhuman primates have reported a left visual preference (right hemisphere dominance) during aggressive encounters in gelada baboons (Casperd and Dunbar, 1996) and in a zoo-housed group of mangabeys during spontaneous approach behaviors (Baraud et al., 2009), suggesting that rudimentary primitive avoidance behaviors controlled by the right hemisphere may have contributed to the emergence of negative emotions (Vallortigara and Rogers, 2005; Vallortigara et al., 2011).

Evidence from great ape studies has highlighted the importance of the social environment in modulating behavior during social interactions and situations involving increased arousal. High-ranking chimpanzees were approached significantly more frequently from their left visual hemifield suggesting the facilitation for the rapid identification of facial expressions and predictability of behaviors by the right hemisphere (Fernández-Carriba et al., 2002). Left biased motor asymmetries have also been associated with self-directed behaviours. For example, rehabilitated orangutans exhibited a significant group-level lateralized preference for left-handed scratching and for the fine manipulation of parts of the face (Rogers and Kaplan, 1995), and while self-directed scratching showed no hand preference in chimpanzees, there was a significant bias for scratching on the left side of the body (Hopkins, 2006). Forrester and colleagues (2011; 2012) noted an increase in left hand (right hemisphere) activity during the observation of naturalistic unimanual hand actions for self-directed behaviors and hand actions directed towards social partners compared with hand actions directed towards objects. In all cases, the authors postulated a right hemisphere dominant role in the processing of emotive and arousal-increasing stimuli.

A recent study by Quaresmini et al. (2014) aligns most closely with the evolution of social lateralization studies that indicate a preference to keep conspecifics proximally situated with a left visual field advantage during spontaneous natural behaviors. Observational focal sampling of spontaneous social behaviors in a family group of western lowland gorillas (Gorilla gorilla gorilla) and in a colony of captive zoo-living chimpanzees (Pan troglodytes), revealed group-level biases in both gorillas and chimpanzees (trend) for keeping conspecifics proximally situated to the left side of the focal individual compared with the right side. The authors suggest that lateral

positioning is likely to reflect a right hemisphere specialization for a heightened state of arousal associated with the detection of faces and facial expressions. These studies support the evolutionary perspective that the right hemisphere retains dominant control for behaviors associated with individual recognition, decoding other's intentions, and navigating the social hierarchical system (for a review, see Rosa Salva, et al., 2012). Moreover, findings from these studies suggest that the social environment may have been a critical pressure in aligning population behavior for predator defense and for cooperation (Ghirlanda et al., 2009; Ghirlanda and Vallortigara, 2004; Vallortigara and Rogers, 2005).

The study of human emotion processing has a long history in the literature, dominated by two prevailing theories of cerebral lateralization. The right hemisphere hypothesis (e.g. Borod et al., 1998; Campbell, 1982) proposes that the right hemisphere is solely responsible for the processing of emotion. Alternatively, the valence hypothesis (e.g. Davidson, 1995) purports that both the right and the left hemispheres are involved in affect processing, such that the left hemisphere is dominant for positive affect and the right hemisphere is dominant for negative affect. Although animal studies do not contradict the right hemisphere theory from an evolutionary perspective, evidence from non-human animal approach/avoidance behaviors tend to be more parsimonious with the valence theory. For example, birds (Franklin III and Lima, 2001; Koboroff et al., 2008; Rogers, 2000b), lizards (in the laboratory: Bonati et al., 2013; in the wild: Martín et al., 2010), and toads (Lippolis et al., 2002), have all been shown to manifest a left eye preference for well-learned sequences of actions (e.g. predator monitoring), but conversely, they demonstrate a rightward preference for responding to urgent situations (e.g. escaping from the dangerous stimulus). Additionally, in great apes, a

recent eye preference study found a left visual field /right hemisphere advantage for negative stimuli and right visual field/left hemisphere advantage for positive stimuli for viewing pictures (Braccini et al., 2012).

In humans, the valence theory model has gained some support from laboratory investigations. For example, the right hemisphere demonstrated greater activation than the left hemisphere in the region of the superior temporal sulcus associated with the processing of an approaching stranger with directed mutual gaze (Pelphrey et al., 2004). Additionally, right-handed people have been shown to respond more quickly to unexpected stimuli with their left hand compared with their right hand (e.g. Fox et al., 2006 reference). And, nonverbal, emotional vocalizations (e.g. cries and shouts) have demonstrated a right-hemisphere activation dominance in contrast to emotionally neutral vocalizations, which were biased to the left hemisphere (for a review see, Scott et al., 2009). Moreover, studies of brain damaged individuals suggest that people who incur left hemisphere trauma are more likely to become depressed than those who incur injury to the right hemisphere (e.g. MacHale et al., 1998). One theory is that the right hemisphere possesses a sensitive attentional system that responds selectively for novel and dangerous stimuli in the environment (for a review see Fox et al., 2006).

Social laterality has been little studied in the naturalistic behaviours of humans. The data that exists in this area suggest that mothers and fathers prefer to position their offspring on left side of their bodies (Nakamichi and Takeda, 1995; Scola and Vauclair, 2010a; Vauclair and Scola, 2009). While it is not proven that left arm cradling is associated with cerebral lateralization for the perception of emotion, the

physical positioning is thought to enable social-emotional feedback stimuli (e.g. gaze, facial expression) to maintain a direct route to the right hemisphere (for a review, see Scola and Vauclair, 2010b). This interpretation gains support from a study that indicated that children who were held with a left arm preference demonstrated a typical left visual field (right hemisphere) bias for faces on chimeric face tests, whereas individuals who were held with a right-arm lacked a visual field bias (Vervloed, et al., 2011). The ramification of hemispheric bilateralization for social-emotional processing has yet to be explored within the scope of cognitive development.

The influence of the social environment on lateralized behaviors has now been investigated across a wide variety of animal species. New evidence suggests that the social environment elicits lateralized motor behavior. Currently, there is a paucity of data relating to how humans navigate their environmental space, and investigations that consider the naturalistic context of the individual are rare. The current study provides the first report of lateralized social behaviors elicited by two populations of human children during naturalistic play. Extending upon human and animal studies of social laterality, this study observed the natural and spontaneous lateral navigational routes of children around adults, peers and objects in order to consider cerebral lateralization and lateralized motor action within the social environment.

2. Methods

2.1 Participants

All of the participants were observed unobtrusively in a naturalistic environment using an opportunity sampling method. Data relating to gender, age and handedness were not recorded. Only children were included in the study because it limits the influence of learnt social and cultural conventions. The procedures for this study involving human participants were in accordance with ethical standards of the responsible committee on human experimentation (institutional and national) and with the spirit of the Helsinki Declaration of 1975, as revised in 2000.

2.1.1 Participants C-Population

C-Population consisted of 101 individuals. Individuals were observed within a public play area, which contained equipment suitable for children up to a maximum of fourteen years of age.

2.1.2 Participants M-Population

M-Population consisted of approximately 200 children aged between four and eleven years. Individuals were observed within a school playground, (St Catherine's Primary School, Kent) which contained equipment suitable for children school children aged between 5-11 years.

2.2 Data capture

The study considered the observed naturalistic play behaviours of two separate populations of children (C-Population and M-Population) at different sites on

different dates and independently coded by two different raters (C and M). Data for C-Population were collected between March and April in 2013, while data for M-Population were collected between the January and February 2014.

Children were observed during naturalistic play for the assessment of navigational behaviours within the social environment. C-Population data were recorded over 3 visits for an average of 60 minutes visit, equalling a total of approximately 180 minutes and 340 events. M-Population data were recorded over 7 visits for an average of 25 minutes per visit equalling a total of 175 minutes and 348 events.

2.3 Data Coding

Two independent raters recorded observational data (C, M). Only information specifically related to lateral direction on a sagittal plane was recorded. A pen and paper recording method was adopted using a preformatted spread-sheet indicating variables to be recorded. The lateral path (left, right) that the observed child chose to navigate around stationary target (peer, adult, object) on order to reach a position accessible by a clear path on both sides and of approximately equal distance achieved by a left or right path was noted (Figure 1).

Figure 1.

- Insert Figure 1 -

Figure 1 illustrates the two possible navigational paths (left, right) of the observed child around a target (in this case a peer). A left or right navigational path inherently dictates the side of the body that will be presented to the individual around which the observed child navigates. In this case, a left navigational path presents the right side of the body and right visual field to the peer. A right navigational path presents the left side of the body and the left visual field to the peer.

Navigation around both peers and adults was considered. Additionally, a control condition was employed utilizing fixed, inanimate objects (e.g. large rubbish bin) in order to create the following 2x3 factor design: navigate left (adult), navigate left (peer), navigate left (object), navigate right (adult), navigate right (peer), navigate right (object). To control for confounding factors, each navigational path of an observed child began at a neutral point (approximately equidistant left or right from the desired location), and proceeded around (left or right) one of the target categories (adult, peer, object). The observed child and the target (peer, adult) were required to have directed gaze. If the observed child was navigating around a peer or adult that was facing away (gaze averted or obscured), the trial was excluded. Additionally, if a child began navigation from an ambiguous position (i.e. not equidistant from the desired goal location), the event was excluded from the analysis. Each navigational path was equal to one frequency point. In line with Quaresmini et al. (2014), to ensure that the relative presence of the social partner was influencing the positioning of the focal subject, we adopted an approximate distance of less than 3 m or less between the child being observed and the social partners.

Data collection method varied slightly between the two populations of children. For C-Population, a focal sampling approach was employed. Each focal follow lasted two minutes in duration. Data were included to the dataset if two minutes of continuous observation was completed. Stationery object targets consisted of a tree, a rubbish bin and an ornamental rock and remained consistent across all data collection visits. These objects were fixed at the entry point of the playground and required lateral navigation to access the playground equipment. These fixed items were chosen because they presented equal opportunity for navigation around both sides.

M-Population data collection consisted of an opportunity sampling of an entire school population. Each data point was collected based around a stationery target (adult, peer, object) used as a reference location. It was necessary that animate targets remained stationery throughout the observed child's navigational path to their desired location. Stationery object target was a rubbish bin. This object and its location remained consistent throughout all seven data collection visits. The bin was located at the intersection of two discrete segments of the playground, such that it was circumnavigated by the majority of the children during any given play session.

2.4 Data Analysis

A laterality index (LI), binomial tests, z-scores approximations of the binomial scores and a chi-square test were performed to assess population-level lateral biases. Additionally, peer and adult frequencies were collapsed within and between the two populations in order to consider the influence of animate and inanimate targets (e.g. Forrester et al. 2011; 2012; 2013). LI scores were calculated using the formula [LI =

(R-L)/(R+L)], with R and L being the frequency counts for right and left navigational path frequency counts. LI values vary on a continuum between -1.0 and +1.0, where the sign indicates the direction of hand preference. When R=L, then LI is zero. Positive values reflect a right navigational path preference while negative values reflect a left navigational path preference. The absolute value depicts the strength of hand preference. The directional strength of navigational path for each population was calculated using z-scores such that a population were left navigational path biased when $z \leq -1.96$, right navigational path biased when $z \geq 1.96$ and ambi-preferent for path direction when $-1.96 < z < 1.96$. All statistical tests were two-tailed (alpha < .05).

3. Results

Raw frequencies, binomial approximations of z-scores for each population and HI scores are presented in Table 1 by population (M Population, C Population and populations combined). Factors are displayed by target condition (peer, adult, object) and side (left, right).

Table 1 demonstrates raw frequencies, binomial approximations of z-scores and HI scores of unimanual lateralized hand actions.

- Insert Table 1 -

Because the binomial tests indicated that children navigated around both peers and adults with a significant bias of presenting their left side, in both populations, these two levels were collapsed for further statistical tests. A 2x2 chi-square test was

conducted on each population to consider target (human, object) and side (left, right). The M-Population revealed a significant interaction between target and side such that the children were biased towards a rightward navigational path around a peer, where as navigation around an object did not elicit a lateral bias $\chi^2(1, N = 101) = 5.27$, $p = .022$. Likewise, the C-Population revealed a significant interaction between target and side such that the children were biased towards a rightward navigational path around a peer, where as navigation around an object did not elicit a lateral bias $\chi^2(1, N = 200) = 11.7$, $p = .001$ (Figure 2).

Figure 2.

- Insert Figure 2 -

Figure 2 demonstrates the total frequencies by each population for target type (human, object) and navigation path (left, right).

Since both populations resulted in a significant bias for children choosing a right path to navigate human targets, a further chi-square test was conducted on the pooled data from both populations to demonstrate the robustness of the pattern, $\chi^2(1, N = 301) = 20.22$, $p < .000$ (Figure 3).

Figure 3.

- Insert Figure 3 -

Figure 3 illustrates the total frequencies by the combined population for target type (human, object) and navigation path (left, right).

4. Discussion

The present study considered the lateral navigational paths of children within a naturalistic setting to align with investigations of social lateralization in observational animal studies. Two populations of children were assessed by different observers at different locations, and at different times. Analyses revealed that both populations expressed a significant population-level bias for choosing a rightward navigational path around a human compared with a leftward navigational path. Additionally, neither population expressed a significant bias for a lateral preference when navigating around an object. These findings are to be considered in light of evolutionary theories for cerebral lateralization.

A bias for a right navigational path inherently implies that the navigating child is presenting the stationary target with the left side of the body. This social positing could impact upon both the production and perception of emotion processing. In the first instance, a bias to keep conspecifics on the left side inherently provides an advantage for viewing social stimuli with the left visual field. The left visual field would provide the most efficient route to the right hemisphere for processing identity, intention and angry or fearful facial expressions. This is consistent with animal studies that have demonstrated a left eye/right hemisphere preference bias for to monitoring familiar versus unfamiliar conspecifics (domestic chick: Deng and Rogers, 2002; Vallortigara and Andrew, 1991; Vallortigara et al., 2001; fish: Brown et al.,

2007; Sovrano, 2004; chimpanzees and gorillas: Quaresmini et al. 2014). Additionally, a bias of the left visual field/right hemisphere has been reported in recognizing faces and facial expressions in both apes (Morris and Hopkins, 1993) and humans (De Renzi et al., 1994; Kanwisher et al., 1998). Within this context, exposing the left side of the body to conspecifics might be advantageous during novel or urgent situations to execute physical behaviors for protection and locomotion escape behaviors. In the second instance, the left side of the face in non-human primates has been reported to display emotive expression both earlier and more intensely than the right side of the face (Fernández-Carriba et al., 2002; Hauser, 1993; Hook-Costigan and Rogers, 1998). This lateral positioning may reflect a strategy to clearly display arousal status in order to inhibit extreme aggressive behavioral responses (Baraud et al., 2009).

Although approaching and withdrawing beahviours are well documented across animal species (Davidson et al., 1990; Quaranta et al., 2007; Siniscalchi et al., 2013), little is still known about how this behavior manifests in modern humans. Modern humans represent an animal species with an extremely complex social system. Many of our conscious motor actions related to approaching individuals are shaped and influenced by culture and social convention (e.g. hand shakes, kissing, etc.). However, our automatic motor actions may still represent evolutionary primitive patterns of behavior that are underpinned by cerebral specialization of the two hemispheres. Moreover, the display of these population-level lateralized behaviours (e.g. bias for keeping conspecifics in the left visual field) may be rooted in social species and facilitates the social communication and the prediction of social responses (Ghirlanda and Vallortigara, 2004; Vallortigara and Rogers, 2005).

Studies of cerebral lateralization indicate that the dominant functions are not solely processed by a single hemisphere. For example, studies of processing social stimuli also indicate small contributions from the left hemisphere: Meng et al., 2012), monkeys (Broad et al., 2000; Guo et al., 2009; Hamilton and Vermeire, 1988; Pinsk et al., 2005), dogs (Guo et al., 2009), and sheep (Peirce et al., 2000; Peirce and Kendrik, 2002). Therefore, there are limitations to the extent with which we can attribute a single function to a single hemisphere. Additionally, more detailed studies on lateralized motor biases are necessary at the individual level to shed further light on the association between cerebral lateralization of function and contralateral motor action. Nevertheless, evidence from a wide range of animal species of hemispheric dominance for specific functions has proven to be an informative behavioral marker of brain organization (e.g. MacNeilage et al. 2009).

Understanding how individuals navigate social networks may shed light on how and which environmental pressures helped to shape modern human social behavior. Specifically, the environment may have been a critical pressure in aligning population behavior for social actions requiring cooperation (Ghirlanda et al., 2009; Ghirlanda and Vallortigara, 2004; Vallortigara and Rogers, 2005). Additionally, future studies may consider the evaluation of the cognitive abilities of individuals with lateralized social navigation behaviors compared with individuals who do not express lateralized social navigation behaviors. It has been reported that stronger lateral motor dominance (e.g. handedness) correlates with the successful hemispheric specialization for language (Toga and Thompson, 2003). The present findings suggest that the environment elicits predictable behavior for social navigation that facilitates both the

production and perception of social-emotion stimuli in typically developing children. Therefore, the identification of individuals lacking lateralized social navigations behaviors may allow for the early targeting of individuals with cognitive delays and/or disorders.

Acknowledgements

We are grateful to the parents, teachers and children of St. Catherine's Primary School, Kent, for their participation in this investigation. Additionally, we gratefully acknowledge funding support provided in part the University of Westminster's Psychology Publication Stimulus Scheme.

References

1. Baraud, I., Buytet, B., Bec, P., Blois-Heulin, C., 2009. Social laterality and 'transversality' in two species of mangabeys: Influence of rank and implication for hemispheric specialization. Behavioural Brain Research, 198, 449–458. doi:10.1016/j.bbr.2008.11.032
2. Bonati, B., Csermely, D., Sovrano, V.A., 2013. Looking at a predator with the left or right eye: Asymmetry of response in lizards. Laterality: Asymmetries of Body. Brain and Cognition. 18, 329–339. doi:10.1080/1357650X.2012.673623
3. Borod, J.C., Cicero, B.A., Obler, L.K., Welkowitz, J., Erhan, H.M., Santschi, C., . . . Whalen, J.R., 1998. Right hemisphere emotional perception: Evidence across multiple channels. Neuropsychology. 12, 446–458. doi:10.1037/0894-4105.12.3.446

4. Braccini, S.N., Lambeth, S.P., Schapiro, S.J., Fitch, W.T., 2012. Eye preferences in captive chimpanzees. Animal Cognition. 15, 971–978. doi:10.1007/s10071-012-0523-9
5. Broad, K.D., Mimmack, M.L., Kendrick, K.M., 2000. Is right hemispheric specialization for face discrimination specific to humans? European Journal of Neuroscience
6. Brown, C., Western, J., Braithwaite, V.A., 2007. The influence of early experience on, and inheritance of, cerebral lateralization. Animal Behaviour. 74, 231-238. doi: 10.1016/j.anbehav.2006.08.014
7. Burt, D.M., Perret, D.I., 1997. Perceptual asymmetries in judgments of facial attractiveness, age, gender, speech and expression. Neuropsychologia. 35, 685–693. doi:10.1016/S0028-3932(96)00111-X
8. Campbell, R., 1982. Asymmetries in moving faces. British Journal of Psychology. 73, 95–103. doi:10.1111/j.2044-8295.1982.tb01794.x
9. Casperd, J.M., Dunbar, R.I.M., 1996. Asymmetries in the visual processing of emotional cues during agonistic interactions by gelada baboons. Behavioural Processes. 37, 57–65. doi:10.1016/0376-6357(95)00075-5
10. Daisley, J.N., Regolin, L., Vallortigara, G., 2010. Logic in an asymmetrical (social) brain: Transitive inference in the young domestic chick. Social Neuroscience. 5, 309–319. doi:10.1080/17470910903529795
11. Davidson, R.J. 1995. Cerebral asymmetry, emotion, and affective style, in: Davidson, R.J., Hugdahl, K. (Eds.), Brain asymmetry. MIT Press, Cambridge, MA, pp. 361–387.
12. Davidson, R.J., Ekman, P., Saron, C.D., Senulis, J.A., Friesen, W.V., 1990. Approach-withdrawal and cerebral asymmetry: Emotional expression and brain

physiology I. Journal of Personality and Social Psychology. 58, 330–341. doi:10.1037/0022-3514.58.2.330

13. De Renzi, E., Perani, D., Carlesimo, G.A., Silveri, M.C., Fazio, F., 1994. Prosopagnosia can be associated with damage confined to the right hemisphere: An MRI and PET study and a review of the literature. Neuropsychologia. 32, 893–902. doi:10.1016/0028-3932(94)90041-8
14. De Santi, A., Sovrano, A., Bisazza, G., Vallortigara, G. 2001. Mosquitofish display differential left- and right-eye use during mirror-image scrutiny and predator-inspection responses. Animal Behaviour. 61, 305-310.
15. Deckel, A.W., 1995. Lateralization of aggressive responses in Anolis. Journal of Experimental Zoology. 272, 194–200.
16. Deng, C., Rogers, L.J., 1997. Differential contributions of the two visual pathways to functional lateralization in chicks. Behavioural Brain Research. 87:173–82.
17. Fernández-Carriba, S., Loeches, A., Morcillo, A., Hopkins, W.D., 2002. Functional asymmetry of emotions in primates: New findings in chimpanzees. Brain Research Bulletin. 57, 561–564. doi:10.1016/S0361-9230(01)00685-2
18. Forrester, G.S., Leavens, D.A., Quaresmini, C., Vallortigara, G., 2011. Target animacy influences gorilla handedness. Animal Cognition. 14, 903–907. doi:10.1007/s10071-011-0413-6
19. Forrester, G.S., Quaresmini, C., Leavens, D.S., Spiezio, C., Vallortigara, G., 2012. Target animacy influences chimpanzee handedness. Animal Cognition. 15(6):1121-7.

20. Fox, M.D., Corbetta, M., Snyder, A.Z., Vincent, J.L., Raichle, M.E., 2006. Spontaneous neuronal activity distinguishes human dorsal and ventral attentional systems. PNAS. 103(35):10046–10051. doi**:**10.1073/pnas.0606682103
21. Frasnelli, E., Vallortigara, G., Rogers, L.J., 2012. Left-right asymmetries of behaviour and nervous system in invertebrates. Neuroscience & Biobehavioral Reviews. 36, 1273–1291. doi:10.1016/j.neubiorev.2012.02.006.
22. Franklin III, W.E., Lima, S.L., 2001. Laterality in avian vigilance: Do sparrows have a favourite eye? Animal Behaviour. 62, 879–885. doi:10.1006/anbe.2001.1826
23. Ghirlanda, S., Vallortigara, G., 2004. The evolution of brain lateralization: A game theoretical analysis of population structure. Proceedings of the Royal Society B: Biological Sciences. 271, 853–857. doi:10.1098/rspb.2003.2669
24. Ghirlanda, S., Frasnelli, E., Vallortigara, G., 2009. Intraspecific competition and coordination in the evolution of lateralization. Philosophical Transactions of the Royal Society B: Biological Sciences. 364, 861–866. doi:10.1098/rstb.2008.0227
25. Guo, K., Meints, K., Hall, C., Hall, S., Mills, D., 2009. Left gaze bias in humans, rhesus monkeys and domestic dogs. Animal Cognition. 12, 409–418. doi:10.1007/s10071-008-0199-3
26. Hamilton, C.R., Vermeire, B.A., 1988. Complementary hemispheric specialization in monkeys. Science. 242, 1691–1694. doi:10.1126/science.3201258
27. Hauser, M.D., 1993. Right hemisphere dominance for the production of facial expression in monkeys. Science. 261, 475–477. doi:10.1126/science.8332914
28. Hews, D.K., Worthington, R.A., 2001. Fighting from the right side of the brain: Left visual field preference during aggression in free-ranging male lizards

519 (Urosaurus ornatus). Brain, Behavior and Evolution. 58, 356–361.
520 doi:10.1159/000057576
521 29. Hook-Costigan, M.A., Rogers, L.J., 1998. Lateralized use of the mouth in
522 production of vocalizations by marmosets. Neuropsychologia. 36, 1265–1273.
523 doi:10.1016/S0028-3932(98)00037-2
524 30. Hopkins W.D., 2006. Lateralized Scratching in Chimpanzees (Pan troglodytes):
525 Evidence of a Functional Asymmetry During Arousal. Emotion. 6(4), 553-559.
526 31. Hopkins, W.D., 2004. Laterality in maternal cradling and infant positional biases:
527 Implications for the development and evolution of hand preferences in nonhuman
528 primates. International Journal of Primatology. 25, 1243–1265.
529 doi:10.1023/B:IJOP.0000043961.89133.3d
530 32. Kanwisher, N., Tong, F., Nakayama, K., 1998. The effect of face inversion on the
531 human fusiform face area. Cognition. 68, B1–B11. doi:10.1016/S0010-
532 0277(98)00035-3
533 33. Karenina, K., Giljov, A., Baranov, V., Osipova, L., Krasnova, V., Malashichev,
534 Y. 2010. Visual laterality of calf-mother interactions in wild whales. PLoS One,
535 5, e13787. doi:10.1371/journal.pone.0013787
536 34. Koboroff, A., Kaplan, G., Rogers, L.J. 2008. Hemispheric specialization in
537 Australian magpies (Gymnorhina tibicen) shown as eye preferences during
538 response to a predator. Brain Research Bulletin. 76, 304-306.
539 doi:10.1016/j.brainresbull.2008.02.015
540 35. Leavens, D.A., Aureli, F., Hopkins, W.D. 2004. Behavioral evidence for the
541 cutaneous expression of emotion in a chimpanzee (Pan troglodytes). Behaviour.
542 141, 979–997. doi:10.1163/1568539042360189

543 36. Lippolis, G., Bisazza, A., Rogers, L.J., Vallortigara, G., 2002. Lateralisation of
544 predator avoidance responses in three species of toads. Laterality: Asymmetries
545 of Body, Brain and Cognition. 7, 163–183. doi:10.1080/13576500143000221
546 37. Machale, S.M., O'Rourke, S.J., Wardlaw, J.M., Martin, S.D., 1998. Depression
547 and its relation to lesion location after stroke. Journal of Neurology,
548 Neurosurgery & Psychiatry. 64, 371-375. doi:10.1136/jnnp.64.3.371
549 38. MacNeilage, P.F., Rogers, L.J., Vallortigara, G., 2009. Origins of the left and
550 right brain. Scientific American. 301, 60–67.
551 doi:10.1038/scientificamerican0709-60
552 39. Martín, J., López, P., Bonati, B., Csermely, D., 2010. Lateralization when
553 monitoring predators in the wild: A left eye control in the common wall lizard
554 (Podarcis muralis). Ethology. 116, 1226–1233. doi:10.1111/j.1439-
555 0310.2010.01836.
556 40. Meng, M., Cherian, T., Singal, G., Sinha, P. 2012. Lateralization of face
557 processing in the human brain. Proceedings of the Royal Society B: Biological
558 Sciences. 279, 2052–2061. doi:10.1098/rspb.2011.1784
559 41. Morris, R.D., Hopkins, W.D., 1993. Perception of human chimeric faces by
560 chimpanzees: Evidence for a right hemisphere advantage. Brain and Cognition.
561 21, 111–122. doi:10.1006/brcg.1993.1008
562 42. Nagy, M., Àkos, Z., Biro, D., Vicsek, T., 2010. Hierarchical group dynamics in
563 pigeon flocks. Nature. 464, 890 – 893. doi:10.1038/nature08891
564 43. Nakamichi, M., Takeda, S., 1995. A child-holding thought experiment: Students
565 prefer to imagine holding an infant on the left side of the body. Perceptual and
566 Motor Skills. 80, 687–690.

44. Peirce, J.W., Kendrik, K.M., 2002. Functional asymmetry in sheep temporal cortex. Neuroreport. 13, 2395–2399. doi:10.1097/00001756-200212200-00004
45. Peirce, J.W., Leigh, A.E., Kendrick, K.M., 2000. Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. Neuropsychologia. 38, 475–483. doi:10.1016/S0028-3932(99)00088-3
46. Pelphrey, K. Al, Viola, R.J., McCarthy, G., 2002. When Strangers Pass: Processing of Mutual and Averted Social Gaze in the Superior Temporal Sulcus. Psychological Science. 15(9), 598-603.
47. Pinsk, M.A., DeSimone, K., Moore, T., Gross, C.G., Kastner, S. 2005. Representations of faces and body parts in macaque temporal cortex: A functional MRI study. PNAS Proceedings of the National Academy of Sciences of the United States of America.102, 6996–7001. doi:10.1073/pnas.0502605102
48. Quaranta, A., Siniscalchi, M., & Vallortigara, G. (2007). Asymmetric tail-wagging responses by dogs to different emotive stimuli. Current Biology. 17, 199-201.
49. Quaresmini, C., Forrester, G.S., Speizio, C., Vallortigara, G., 2014. Social environment elicits lateralized behaviours in gorillas and chimpanzees. Journal of Comparative Psychology. Online First. doi: 10.1037/a0036355
50. Robins, A., Lippolis, G., Bisazza, A., Vallortigara, G., Rogers, L.J., 1998. Lateralized agonistic responses and hindlimb use in toads. Animal Behaviour. 56, 875–881. doi:10.1006/anbe.1998.0877
51. Rogers, L.J., 2000a. Advantages and disadvantages of lateralization, in: Rogers, L.J., Andrew, R.J. (Eds.), Comparative vertebrate lateralization. Cambridge University Press. Cambridge, pp. 126–153.

591 52. Rogers, L.J., 2000b. Evolution of hemispheric specialization: Advantages and
592 disadvantages. Brain and Language. 73, 236–253. doi:10.1006/brln.2000.2305
593 53. Rogers, L.J., Kaplan, G., 1996. Hand preferences and other lateral biases in
594 rehabilitated orang-utans, Pongo pygmaeus pygmaeus Animal Behaviour. 51, 13–
595 25. doi:10.1006/anbe.1996.0002
596 54. Rogers L.J., Zucca P., Vallortigara G., 2004. Advantages of having a lateralized
597 brain. Proceedings of the Royal Society. B;271(6), S420–2.
598 55. Rogers, L.J., Vallortigara, G., Andrew, R.J., 2013. Divided brains. The biology
599 and behaviour of brain asymmetries. Cambridge University Press, New York,
600 NY. doi:10.1017/CBO9780511793899
601 56. Rosa Salva, O., Regolin, L., Mascalzoni, E., Vallortigara, G., 2012. Cerebral and
602 behavioural asymmetry in animal social recognition. Comparative Cognition &
603 Behavior Reviews. 7, 110–138. doi:10.3819/ccbr.2012.70006
604 57. Rutherford, H.J.V., Lindell, A.K., 2011. Author reply: More than evaluation:
605 Lateralization of the neural substrates supporting approach and avoidance
606 motivational systems. Emotion Review. 3, 347–348.
607 doi:10.1177/1754073911402404
608 58. Salk, L., 1960. The effects of normal heartbeat sound on the behavior of the
609 newborn infant: Implications for mental health. World Mental Health. 12, 168–
610 175.
611 59. Scola, C., 2009. L'importance de la relation me`re-enfant sur le coˆte. de portage
612 d'un jeune enfant [The importance of mother–infant relationship for holding-side
613 preferences]. Enfance. 61, 433–457.
614 60. Scola, C., Vauclair, J., 2010a. Infant's holding side biases by fathers in maternity
615 hospitals. Journal of Reproductive and Infant Psychology. 28, 3–10.

61. Scola, C., Vauclair, J., 2010b. Is infant holding-side bias related to motor asymmetries in mother and child? Developmental Psychobiology. 52, 475–486.
62. Scott, S.K., Sauter, D., McGettigan, C., 2009. Brain mechanisms for processing perceived emotional vocalizations in humans, in: Brudzynski S.M. (Ed), Handbook of mammalian vocalization: An integrative neuroscience approach. Academic Press, London, pp. 187-198.
63. Siniscalchi et al. (2013). Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. Current Biology, 23: 2279-2282.
64. Sovrano, V.A., (2004). Visual lateralization in response to familiar and unfamiliar stimuli in fish. Behavioural Brain Research. 152, 385–391. doi:10.1016/j.bbr.2003.10.022
65. Sovrano, V., Bisazza, A., Vallortigara, G., 2001. Lateralization of response to social stimuli in fishes: A comparison between different methods and species. Physiology & Behavior. 74, 237–244. doi:10.1016/S0031-9384(01)00552-2
66. Toga, A.W., Thompson, P.M., 2003. Mapping brain asymmetry. Nature Reviews Neuroscience. 4,37–48.
67. Tommasi, L., 2009. Mechanisms and functions of brain and behavioural asymmetries. Philosophical Transactions of the Royal Society B. 364, 855–9.
68. Vallortigara, G., 1992. Right hemisphere advantage for social recognition in chicks. Neuropsychologia. 30, 761–768. doi:10.1016/0028-3932(92)90080-6
69. Vallortigara, G., Andrew, R.J., 1991. Lateralization of response to change in a model partner by chicks. Animal Behaviour. 41, 187–194. doi:10.1016/S0003-3472(05)80470-1
70. Vallortigara, G., Cozzuti, C., Tommasi, L., Rogers, L.J., 2001. How birds use their eyes: Opposite left-right specialization for the lateral and frontal visual

641 hemifield in the domestic chick. Current Biology. 11, 29–33. doi:10.1016/S0960-
642 9822(00)00027-0
643 71. Vallortigara, G., Rogers, L.J., 2005. Survival with an asymmetrical brain:
644 Advantages and disadvantages of cerebral lateralization. Behavioral and Brain
645 Sciences. 28, 575–589. doi:10.1017/S0140525X05000105
646 72. Vallortigara, G., Chiandetti, C., Sovrano, V.A. 2011. Brain asymmetry (animal).
647 Wiley Interdisciplinary Reviews: Cognitive Science. 2, 146-157 DOI:
648 10.1002/wcs.100
649 73. Vervloed, M.P.J., Hendriks, A.W., van den Eijnde, E., 2011. The effects of
650 mothers' past infant-holding preferences on their adult children's face processing
651 lateralisation. Brain and Cognition. 75(3), 248-54. doi:
652 10.1016/j.bandc.2011.01.002
653 74. Wallez, C., Vauclair, J. 2011. Right hemisphere dominance for emotion
654 processing in baboons. Brain and Cognition. 75, 164–169. doi:
655 10.1016/j.bandc.2010.11

Tables

Navigation Path	C-Population	M-Population	Combined
Left around peer	39	32	71
Right around peer	122	65	187
Laterality index	.52	.34	.45
z-score	*6.46*	*3.25*	*7.16*
Binomial	$p < .000$*	$p = .001$*	$p < .000$*
Left around an adult	32	36	68
Right around an adult	77	58	135
Laterality index	.42	.23	.33
z-score	4.21	2.17	4.63
Binomial	$p < .000$*	$p = .029$*	$p < .000$*
Left around an object	34	75	109
Right around an object	38	82	120
Laterality index	0.06	0.05	0.05
z-score	0.35	0.48	0.66
Binomial	$p = .724$, ns	$p = .632$, ns	$p = .509$, ns

B = binomial approximation of z-score, z = z-score, LI = laterality index (* significant, p<.05, two-tailed)

Figure2

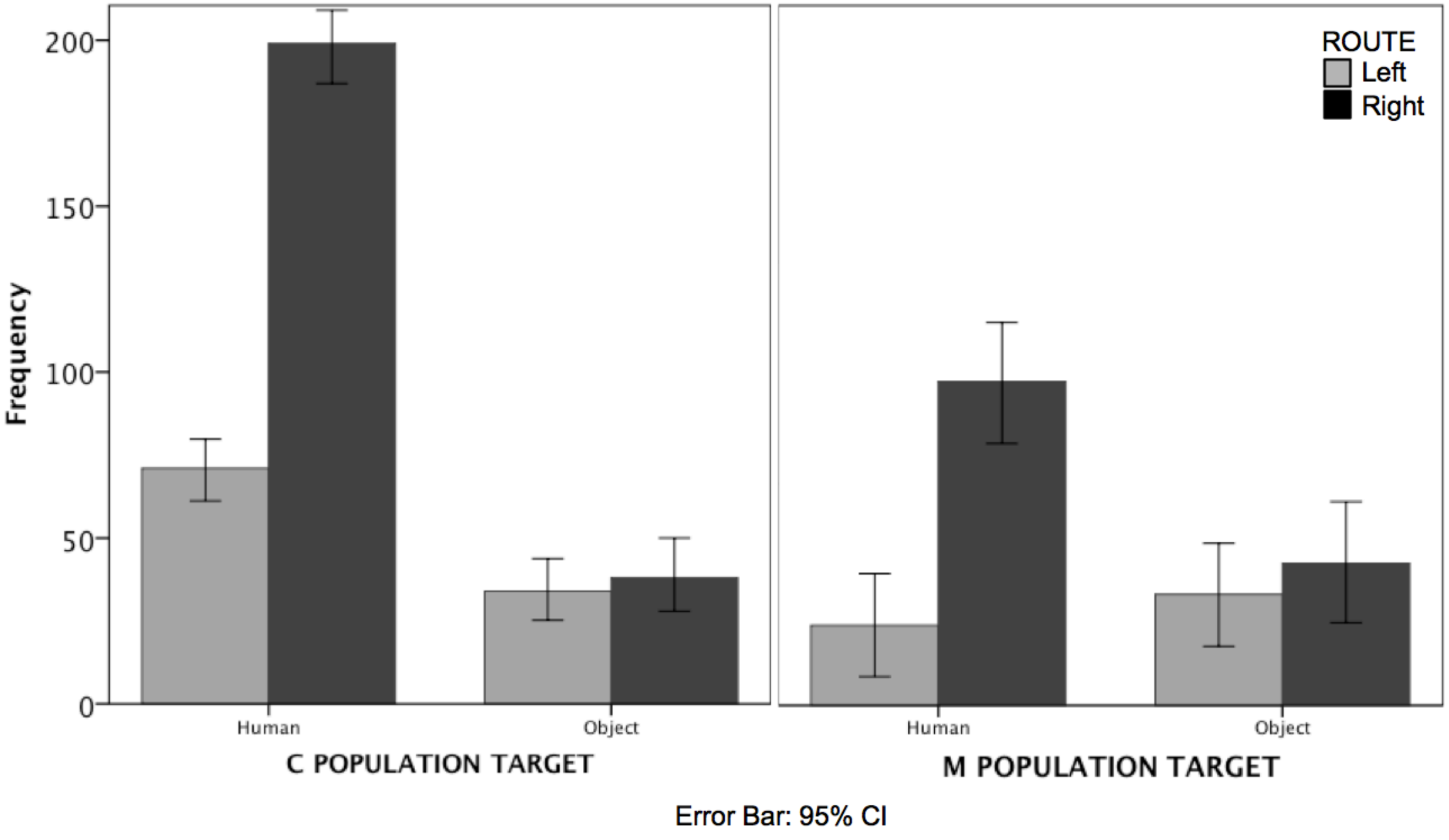
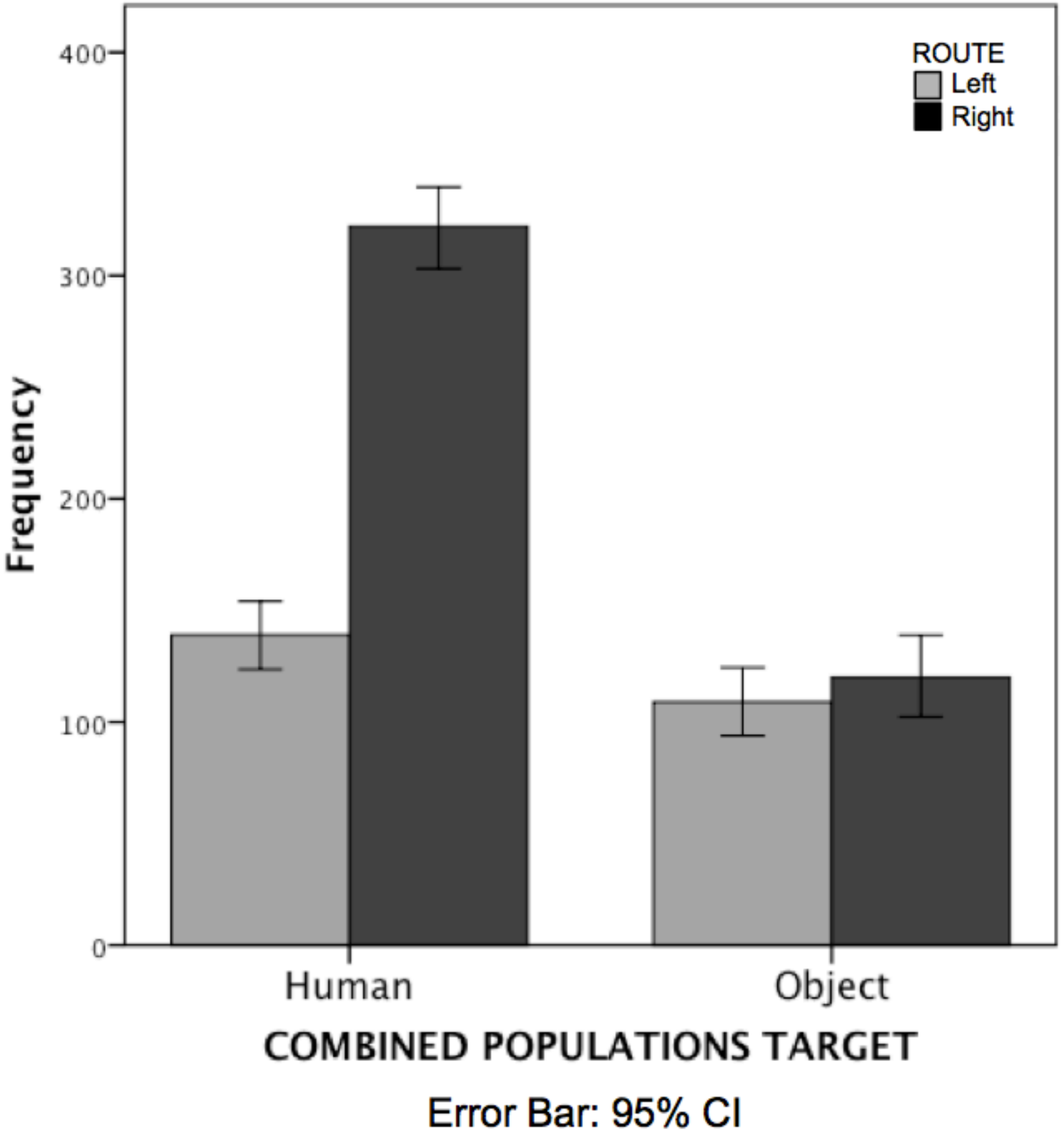

ROUTE
Left
Right
200
150
100
50
0
Frequency
Human
Object
C POPULATION TARGET
Human
Object
M POPULATION TARGET
Error Bar: 95% CI

Figure3


ROUTE
Left
Right
400
300
200
100
0
Frequency
Human
Object
COMBINED POPULATIONS TARGET
Error Bar: 95% CI